

A developmental perspective on evolutionary innovation in the radula of the predatory neogastropod family Muricidae*

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Abstract: The neogastropod family Muricidae includes a diverse set of radular bauplane, including a beaked, three-dimensional form, a flattened-pentacusped form, and a third “dagger” type in which the central rachidian cusp is massive and elongate. Examination of the radular ontogenies of representatives of five muricid subfamilies reveals that several species undergo changes in radular form during ontogeny on a scale comparable to the evolutionary differences between higher taxa. The species *Concholepas concholepas* (Bruguière, 1789) (Rapaninae) and *Trophon geversianus* (Pallas, 1774) (Trophoninae) begin ontogeny with a three-dimensional rachidian characteristic of the Ocenebrinae or Muricopsinae but end with the dagger rachidian typical of their respective subfamilies. Young individuals of *Vitularia salebrosa* (King and Broderip, 1832) (Muricopsinae?) also have a three-dimensional rachidian but shift to a double-dagger morphology by adulthood. *Chicoreus (Phyllonotus) pomum* (Gmelin, 1791) (Muricinae) has a typical flattened muricine rachidian as an adult but possesses a “buccinoid”-like rachidian just after hatching. *Urosalpinx cinerea* (Say, 1822) (Ocenebrinae), was unique among the species examined in exhibiting no ontogenetic changes in radular form. The occurrence of two radular bauplane within the same individual snail during ontogeny suggests great potential for rapid, convergent evolution of adult features through simple changes in developmental timing. A three-dimensional rachidian, for example, could be retained into adulthood through paedomorphosis in any lineage possessing the three-dimensional-to-dagger ontogeny. Systematic assignments of muricids based solely on radular features should be reexamined.

Key words: muricid, rachidian, bauplan, ontogeny, heterochrony

The radulae of a number of gastropod species undergo small to large-scale changes in the number, type, and structural complexity of teeth between the pre-metamorphic larval stage, when the radula first forms, and maturation (references in Fujioka 1984a, Page and Willan 1988, Nybakken 1990, Warén 1990). A controversial but long-standing idea is that such changes in development play a dominant role in the evolutionary origins of new characters, or innovations, and, hence, in the origin of higher taxa (reviewed in Gould 1977). Rather than requiring widespread alteration of structural genes controlling morphology, innovation may derive simply through small-scale changes in regulatory genes controlling the rate and/or timing of development, *i.e.*, heterochrony. Size changes associated with heterochronic evolution may also provide a catalyst for extensive innovation throughout the organism. Changes in skeletal structure, for example, often evolve to compensate for the detrimental by-products of developmental miniaturization (see references in Hanken 1985, Hanken and Wake 1993).

With few exceptions (*e.g.*, Guralnick and Lindberg

1999), however, molluscan biologists have yet to investigate radular evolution from the perspective of development. In the present study, we document radular ontogenies in several taxa belonging to the predatory gastropod family Muricidae and examine the possibility that the evolution of developmental timing has played a central role in the repeated origins of subfamily-level radular bauplane within the Muricidae. Phylogenetic studies are necessary to test the hypothesis that heterochronic mechanisms have been involved in the evolution of any particular structure, but ontogenetic analyses presented herein are a necessary first step.

BACKGROUND

Radular bauplane in the Muricidae

Two nomenclatural schemes have been utilized in the past to describe the basic structural types (referred to throughout this paper as “bauplane”) of the muricid rachidian teeth and to delineate the muricid subfamilies. The first

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system, established by Arakawa (1962, 1964, 1965) and Wu (1965, 1968, 1973), groups muricids according to the number of cusps on the rachidian tooth. These workers subdivided muricid radulae into two classes—a complex “pentacused” rachidian having a central cusp, two lateral cusps, and two marginal cusps, and a simplified “tricused” rachidian having only the central and two lateral cusps (Fig. 1). Fujioka (1985a) later added a third class for taxa having a “monocused” rachidian (*i.e.*, only a central cusp) and recognized a number of intermediate classes as well. As noted by Kool (1987), however, this system suffered from the rather arbitrary manner in which it was applied and is no longer used. For example, some authors counted only major cusps but others counted both cusps and denticles. The variable size, position, and number of cusps and denticles in different muricids make this system impossible to apply unambiguously (Kool 1987).

An alternative system, built upon in this paper, was developed by Vokes (1971), Radwin and D’Attilio (1971, 1976), and D’Attilio (1980, 1991) and is based largely upon variation in the morphology of the most prominent structure on the rachidian—the central cusp—rather than the number of cusps on the tooth. In the “flattened” type, the rachidian is broad, with all the cusps lying in the same plane and the central cusp being slightly longer than either of the

laterals (Fig. 2M). This type occurs in almost all species presently assigned to the subfamilies Muricinae, Typhinae, Tripterotyphinae, and Haustriinae, as well as in many species currently assigned to the Trophoninae and the *Murexsul-Muricopsis* genus group of the Muricopsinae (Radwin and D’Attilio 1971, 1976, Vokes 1971) (Figs. 2A-L). Because the Muricinae predate all other muricid subfamilies by at least 20 million years (see Vokes 1971, 1990, 1992, 1994, Garvie 1991, 1992, Marko and Vermeij 1999, Merle 1999, Vermeij and Carlson 2000), and because the anatomical condition of the Muricinae is likely primitive within the Muricidae (Harasewych 1984), the flattened rachidian type of muricines and other muricids is presumably the plesiomorphic condition for the family.

In a second type, which Vokes (1971) referred to as “three-dimensional” or “3-D,” the rachidian base is narrow (Fig. 3J) and rectangular, with a short, beak-like central cusp that projects up to 90 degrees away from the rachidian base and up to 45 degrees away from either lateral cusp (Fig. 3I). Vokes (1971) and Radwin and D’Attilio (1971) have used terms such as “triangular harrow,” “cowl-like,” and “fang-like” to describe this type as well. A 3-D rachidian type characterizes Vokes’ (1971) *Murexiella* genus group of the Muricopsinae (= *Favartia*/*Pygmaepterys* subclade of Merle and Houart 2003), some species of *Muricopsis* (see Radwin

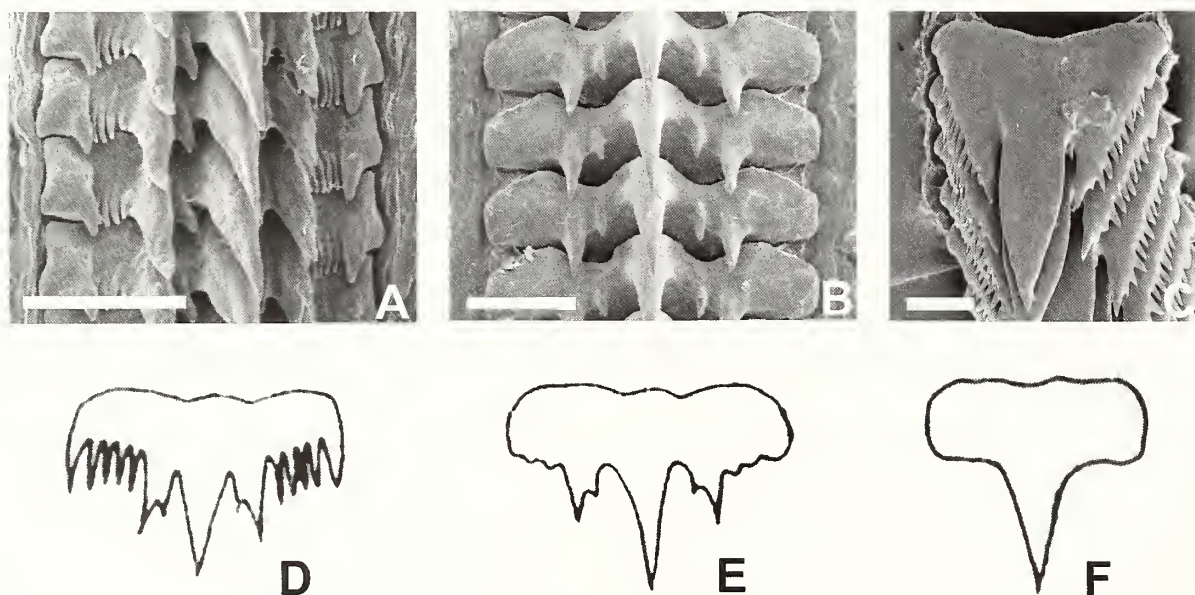


Figure 1. Pentacused, tricused, and monocused rachidian bauplane of Arakawa (1962, 1964, 1965), Wu (1965, 1968, 1973), and Fujioka (1985a). A. The pentacused rachidian characterized by the rapanine *Neothais harpa* (Conrad, 1837), locality: Maui, Hawaiian Islands, scale bar = 50 µm. B. The tricused rachidian characterized by the ergalataxine *Cronia crassulnata* (Hedley, 1915), locality: Gulf of Carpentaria, northern Australia, scale bar = 50 µm. C. The monocused rachidian characterized by the rapanine *Drupella elata* Blainville, 1832, Kauai, Hawaiian Islands, scale bar = 20 µm. D-F, penta-, tri-, and monocused rachidia, modified from Fujioka (1985a, fig. 8).

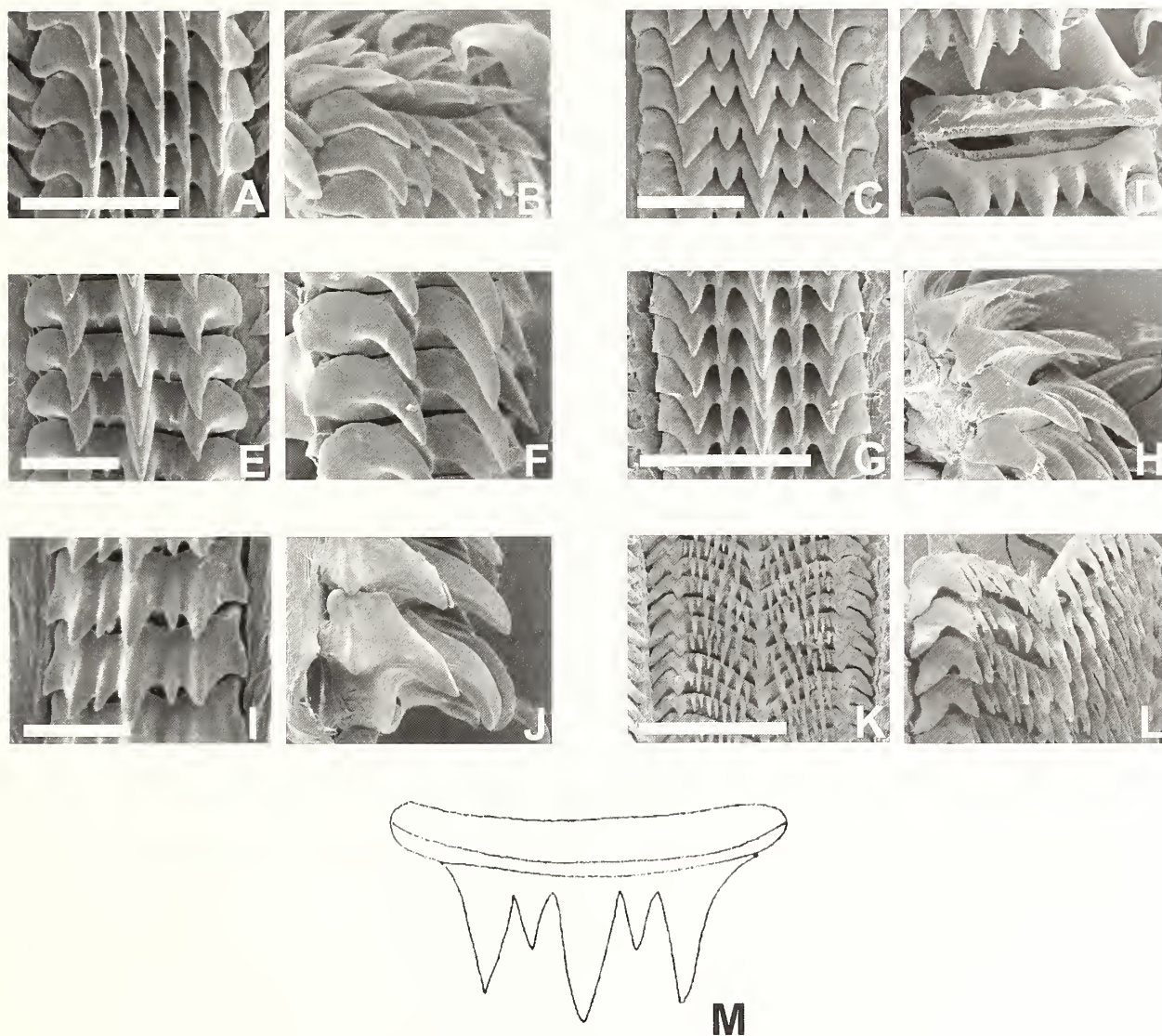


Figure 2. The “flattened” rachidian bauplan. A-B. The muricine *Aspella indentata* Carpenter, 1857, locality: Mira Mar, north of Manzanillo, Mexico, scale bar = 50 μ m. C-D. The muricine *Murex brevispina* var. *macgillivrayi* Dohrn, 1862, locality: Papua New Guinea, scale bar = 100 μ m. E-F. The “trophonine” *Xymenopsis buccineus* (Lamarck, 1816), locality: Tierra del Fuego, Argentina, scale bar = 50 μ m. G-H. The haustriine *Haustrium haustorium* (Gmelin, 1791), locality: New Zealand, scale bar = 100 μ m. I-J. The muricopsine *Murexsul octagonus* Quoy and Gaimard, 1833, locality: New Zealand, scale bar = 50 μ m. K-L. The typhine *Typhisala grandis* (A. Adams, 1855), locality: Golfo de Tehuantepec, Mexico, scale bar = 50 μ m. M. The muricid rachidian bauplan, modified from Vokes (1971, fig. 2a).

and D’Attilio 1976), and the *Ocenebra*-*Ocenebrina* genus group of the *Ocenebrinae* (*sensu* Vermeij and Vokes 1997). Other muricid taxa that possess a beak-like central cusp include the putative-muricopsines *Vitularia* Swainson, 1840; *Acanthotrophon* Hertlein and Strong, 1951; and *Bizetiella* Radwin and D’Attilio, 1972; and the muricine *Chicopinnatus laqueatus* (Sowerby, 1841) (Figs. 3A-H).

In addition to these two general categories of rachidia,

we recognize a third—a “dagger” rachidian—for muricids having a flattened rachidian but modified with a more massive and considerably more elongate central cusp and much weaker lateral and marginal cusps (Fig. 4I). Fujioka’s (1985a) “monocusped” rachidian (Figs. 1C, 1F) is an extreme form of this third type. Muricids possessing a dagger-type rachidian include most rapanine and ergalataxine species as well as the “*Thais*-like” ocenebrines (e.g., *Nucella*

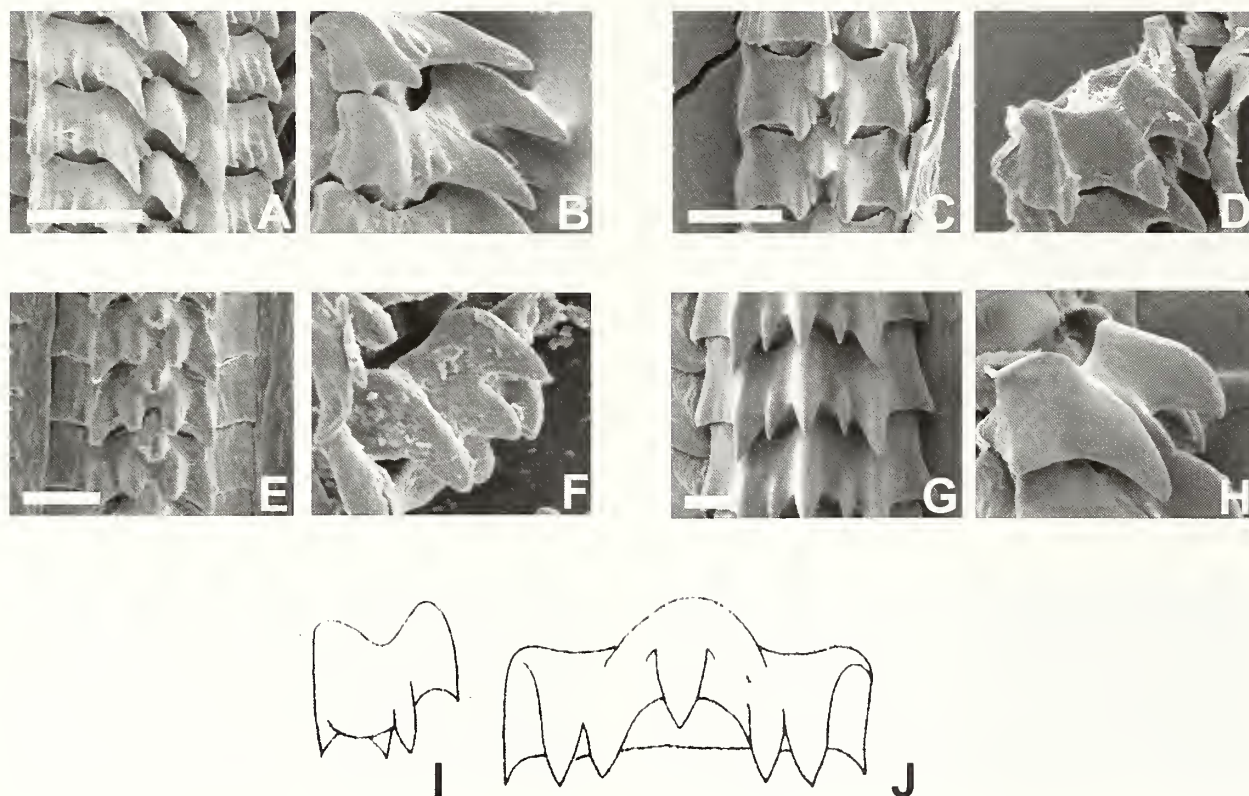


Figure 3. The “three-dimensional” rachidian bauplan. A-B. The ocenebrine *Urosalpinx perrugata* (Conrad, 1846); locality: St. Joseph’s Bay, Florida, scale bar = 50 μ m. C-D. The muricopsine *Caribiella alveata* (Kiener, 1842), locality: Discovery Bay, Jamaica, scale bar = 20 μ m. E-F. The muricopsine *Acanthotrophon sorenseni* Hertlein and Strong, 1951, locality: Gulf of California, Mexico, scale bar = 20 μ m. G-H. The muricine *Chicopinnatus laqueatus* (Sowerby, 1841), locality: Orote Point, Guam, Oceania, scale bar = 20 μ m. I-J. The three-dimensional rachidian bauplan, modified from Vokes (1971, fig. 2b).

Röding, 1798; *Acanthina* Fischer de Waldheim, 1807; etc., see Vermeij and Vokes 1997), *Trophon geversianus* (Pallas, 1774) (type species of the type genus of the Trophoninae), and several problematic South American genera (e.g., *Chorus* Gray, 1847; *Xanthochorus* Fischer, 1884) (Figs. 4A-H).

Researchers have long relied upon these bauplane to assign species to subfamilies and reconstruct muricid phylogeny based on the assumption that the radula is a conservative character complex relative to features of the shell and operculum (Vokes 1964, 1971, Radwin and D’Attilio 1971, 1976, Houart 1992; see additional references in Kool 1987). Vokes (1971), for example, regarded the subfamily Ocenebrinae as phylogenetically nested within the Muricopsinae on the basis of both groups sharing a 3-D rachidian, despite the fact that other morphological features, such as those of the early shell whorls and operculum, support different relationships (Vokes 1971, Kool 1993a, Merle 1999, Vermeij and Carlson 2000). Using the same logic, Radwin and D’Attilio (1976) assigned the genus *Vitularia* to the Muricopsinae, although shell and opercular characters are diffi-

cult to reconcile with this classification (see Vokes 1967, 1977, 1986). Most recently, Bouchet and Houart (1996) re-assigned the muricine *Chicoreus gubbi* (Reeve, 1849) to the Ocenebrinae as a new genus *Chicocenebra* Bouchet and Houart, 1996 based solely on its having a 3-D rachidian, even though its classification as a member of the Muricinae had not been questioned previously when only the shell morphology of this species was known.

Previous studies of radular development and evolution in muricids

If bauplan-level transformations in the muricid radula can occur as a result of small-scale changes in developmental timing, then radular features may be less conservative and, thus, less phylogenetically informative, than is currently thought. At present, the best answer to this question comes from a series of seminal papers by Fujioka (1982, 1984a, 1984b, 1985a, 1985b) on the radulae of the subfamilies Rapaninae and Ergalataxinae. Fujioka found that the lateral cusps, marginal cusps, and intermediate and marginal den-

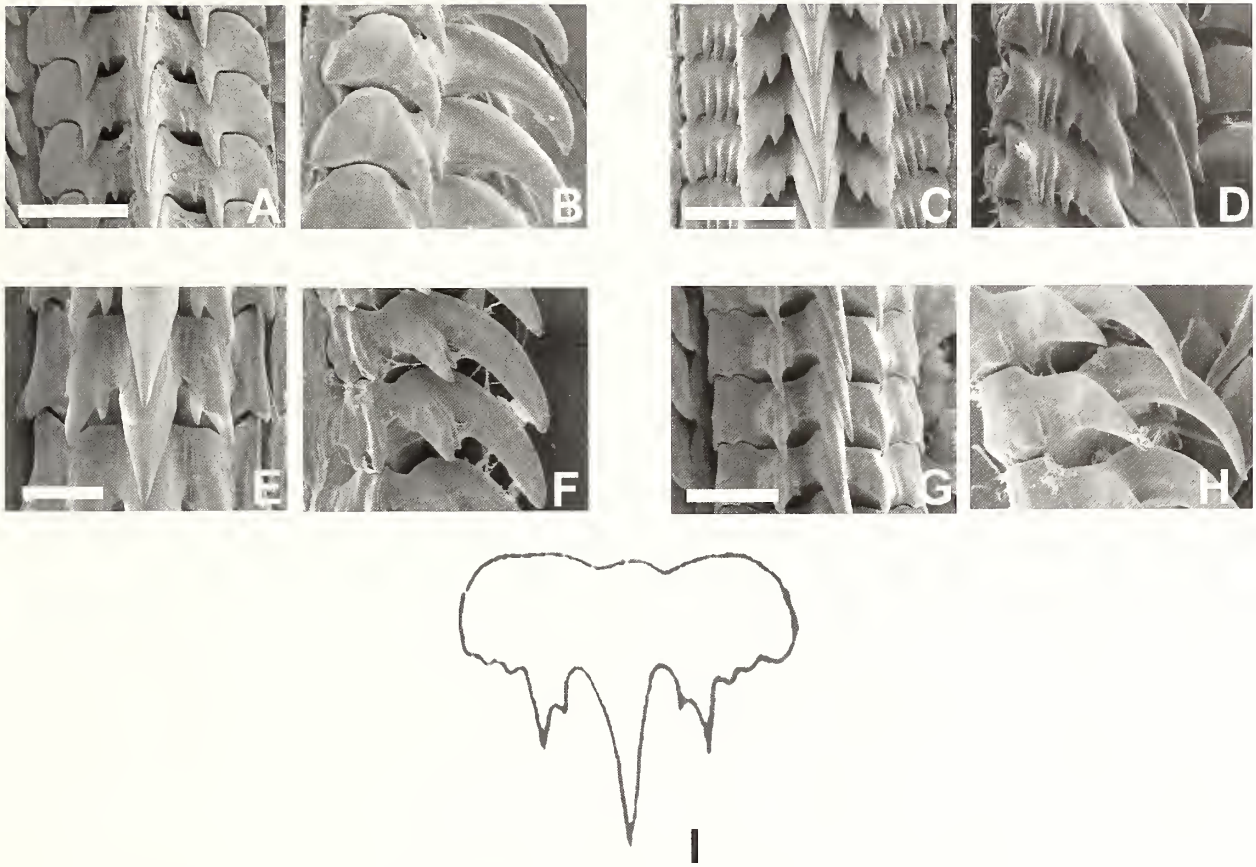


Figure 4. The dagger rachidian bauplan. A-B. The ergalataxine *Cronia* (*Cronia*) *avellana* (Reevem, 1846), locality: western Australia, scale bar = 100 µm. C-D. The rapanine *Agnewia tritoniformis* (Blainville, 1833), locality: Manly, New South Wales, Australia, scale bar = 50 µm. E-F. The ocenebrine *Nucella ostrina* Gould, 1852, locality: Monterey, California, scale bar = 20 µm. G-H. The ergalataxine? *Xanthochorus cassidiformis* Blainville, 1824, locality: Metri Bay, Chile, scale bar = 50 µm. I. The ergalataxine rachidian bauplan, modified from Fujioka (1985a, fig. 8).

ticles in many species of these two subfamilies become progressively atrophied during ontogeny, while the central cusp becomes longer and its base becomes wider.

Rapanines, however, begin ontogeny with a pentacusped rachidian and typically end at the pentacusped or tricusped stage, whereas many of the ergalataxines studied begin ontogeny at the tricusped stage and end with a tricusped or monocusped rachidian. Under the assumption that new characters, such as atrophication, are only added to the end of ontogeny, Fujioka reasoned that the less atrophied pentacusped rachidia of rapanines is the relatively primitive condition and that the ergalataxine condition evolved by peramorphic heterochrony (extended atrophication) of this ancestral ontogeny. Phylogenies published recently for the Rapaninae generally support this evolutionary scenario with ergalataxines depicted as a nested clade within the Rapaninae (i.e., Kool 1993a, Vermeij and Carlson 2000, but see Tan 2003).

More recently, DiSalvo (1988) and DiSalvo and Carriker (1994) documented ontogenetic changes in the rachidian tooth morphology of the rapanine muricid *Concholepas concholepas* (Bruguière, 1789). This species was found to change from a 3-D rachidian in early post-metamorphic animals to a dagger-type rachidian in small sub-adults. Although these workers did not comment on the evolutionary significance of their observations or document the exact size at which this transition occurs, it suggests to us that the 3-D and dagger rachidia in adults could potentially evolve rapidly from one to the other through heterochronic processes.

Focus of the present study

A 3-D rachidian was reported in none of the many juvenile rapanine species studied by Fujioka, which makes its more recently reported occurrence in the rapanine *Concholepas* suspect. Thus, the initial goal of the present study was to test the results of DiSalvo and Carriker by collecting new

early post-larval specimens for *Concholepas concholepas*, verifying their taxonomic identity, and re-examining their early stage radulae using SEM.

The second focus of this paper was to examine the ontogenies of muricids outside of the Rapaninae and Ergalataxinae. With the exception of Houart's (1992) illustration of the radular ontogeny of the muricine *Chicoreus (Triplex) torrefactus* (Sowerby, 1841), there have been no attempts to document ontogenetic series in non-rapanine or non-ergalataxine muricids. Our present study of new and previously collected material allows us to examine for the first time the ontogenies of species representing the Trophoniinae, Ocenebrinae, a second species of the Muricinae, and a putative member of the Muricopsinae.

The third focus of this study was to investigate whether large-scale morphological shifts occur during the earliest ontogenetic stages of development, *i.e.*, between larval metamorphosis and juveniles around 10 mm shell length. Fujioka examined no radulae from early post-metamorphic stage individuals to small juveniles 3 mm in shell length. For more than half the species Fujioka studied, he examined no juveniles smaller than 10 mm in length, and many of his smallest "juveniles" were greater than 25 mm in shell length. DiSalvo's work, in contrast, suggested that changes during earliest ontogeny (*i.e.*, less than 10 mm shell length) may be substantial (DiSalvo 1988, DiSalvo and Carriker 1994) and possibly be related to changes in mode of predation and feeding behavior that can occur within this size range (see discussion section). This study documents the endpoints of the entire ontogenetic sequences beginning with rachidia in earliest post-metamorphic individuals, material permitting.

MATERIALS AND METHODS

Radula preparation

Radulae were recovered from late juvenile and adult alcohol-preserved and dried specimens by dissolving dissected proboscis tissues in a concentrated solution of potassium hydroxide (KOH) for 1-3 days. Radular ribbons, visible with the naked eye, were collected with forceps, rinsed in a series of hot distilled-water washes, fixed to aluminum tabs with double-sided conductive tape, air dried, and gold coated (40 nm thickness) for scanning electron microscopy.

Radulae of early juvenile snails were recovered from dried and alcohol preserved specimens by gently crushing the larval shells in a shallow petri dish filled with a concentrated solution of KOH. After two hours, the dish was heated to 90°C to reverse any precipitation of KOH crystals that might have formed on the radular ribbon. Because they were too small to be collected with forceps, radulae were removed from the KOH solution using a dropper partially filled with

warm distilled water. This was done to dilute the KOH solution collected with the radula and prevent later precipitation of KOH crystals on the radular ribbon during drying. The dilute KOH solution with the radula was then transported by dropper through two rinses of hot distilled water in separate dishes for additional dilution. After two rinses, cleansed radulae were transferred in distilled water by dropper to an aluminum tab coated with double-sided conductive tape and air dried. Aluminum tabs with radulae were gold coated (40 nm thickness). All radulae were examined with an ISI DS-130 scanning electron microscope at the University of California, Davis's Facility for Advanced Instrumentation.

Radula Terminology

Throughout the remainder of this paper, we use the standard terminology illustrated by Radwin and D'Attilio (1976) and Kool (1987, 1993a) to refer to parts of the rachidian radular tooth.

RESULTS

Subfamily RAPANINAE

Concholepas concholepas (Bruguière, 1789)
(Figs. 5A-F)

Material examined

Nineteen juvenile to sub-adult specimens of *Concholepas concholepas* ranging in shell length from 11 to 30 mm were collected in March 2001 from Mehuin, 70 km north of Valdivia, Chile, and placed in 50% ethanol for later dissection. An additional nine early post-metamorphic individuals ranging from 1.7 to 3.9 mm were captured between September 1999 and January 2000 and between January 2000 and August 2000 from artificial collection plates installed at Las Cruces (coast of Santiago Province), Chile, and stored in 50% ethanol.

Ontogeny

In early post-metamorphic juveniles with shell lengths ranging from 1.7 to 3.9 mm, rachidian widths are 20 µm and have a 3-D rachidian morphology (Figs. 5A-D). Most have a single marginal denticle, although the largest individual in this class had two in one marginal area and one in the other (Fig. 5A). The rachidian base end-point is marked by a prominent marginal cusp that runs parallel to the rachidian base. Behind this marginal cusp is a shorter marginal cusp that is poorly developed and bud-like. The two cusps combined loosely resemble the double marginal cusps of the Ocenebrinae.

In young animals with shell lengths between 11 and 13

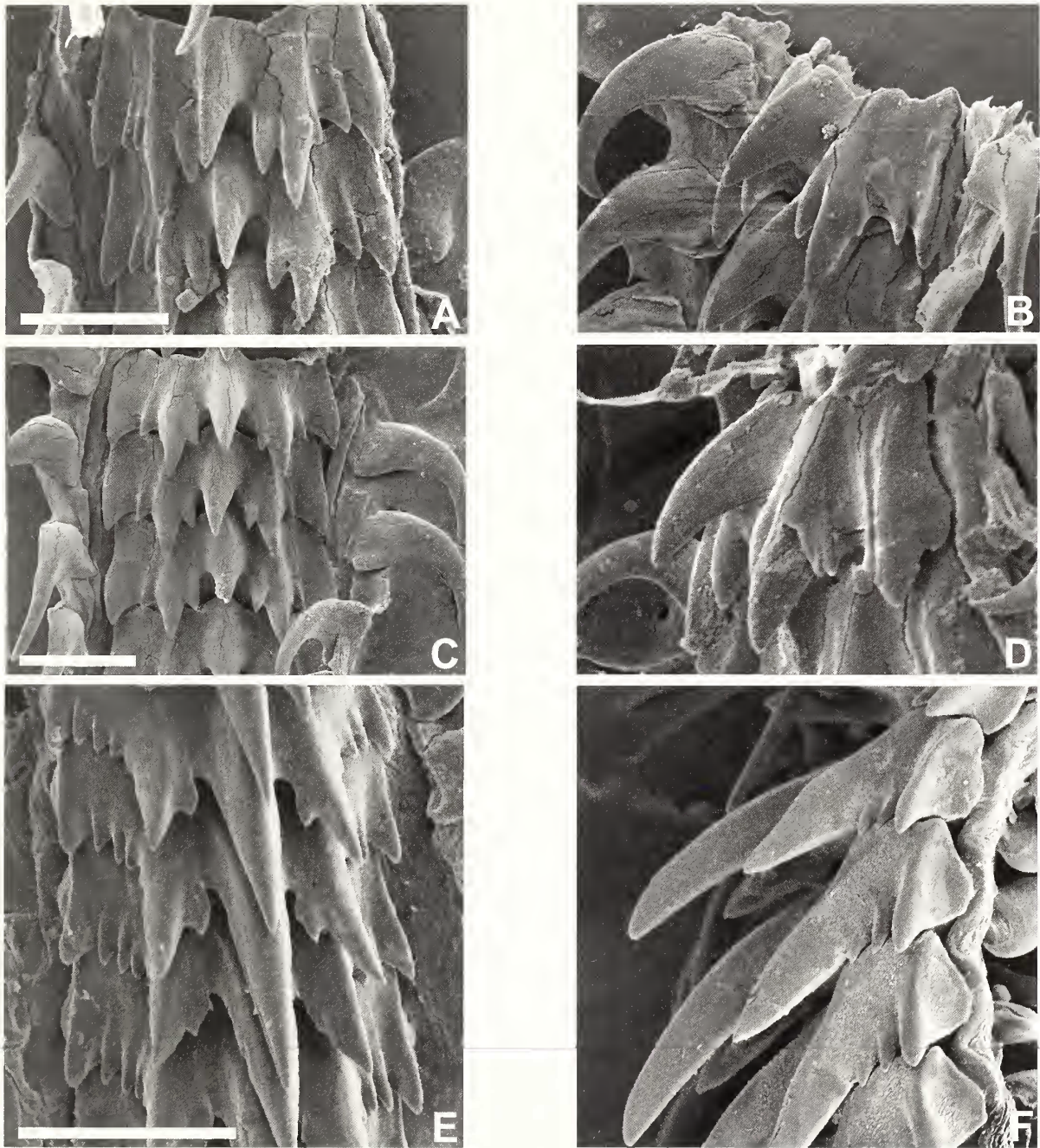


Figure 5. Radular ontogeny of the rapanine muricid *Concholepas concholepas*. A-D. Front and lateral views of rachidia of early post-metamorphic individuals ranging from 1.7 to 3.9 mm in shell length, locality: Las Cruces, Chile, scale bars = 10 μ m. E-F. Front and lateral views of rachidia of a small juvenile with shell length of 15 mm, locality: Mehuin, Chile, scale bar = 50 μ m.

mm, the rachidian tooth increases to approx. 100 μ m in width and assumes the dagger-type morphology (Figs. 5E-F). The lateral cusps are turned outwardly at their distal ends, marginal cusp number increases to two or three, and outer lateral denticles begin to appear. The rachidian base

begins to develop a small, rounded lateral extension at both ends, which may be homologous with the bud-like second marginal cusp observed in the early post-metamorphic juveniles. The radular ontogeny of *Concholepas* is essentially stabilized at the dagger-type rachidian by a shell length of 11

mm with little modification afterwards. Large adults may reach shell lengths upwards of 125 mm. Radulae of larger adult animals are figured elsewhere (Kool 1987, 1993b, DiSalvo 1988) for comparison.

Remarks

DiSalvo (1988) and DiSalvo and Carriker (1994) illustrated the rachidian tooth morphology of the pediveliger stage (1.6-1.9 mm shell length) of the rapanine *Concholepas concholepas* from neustonic pediveliger larvae reared from egg capsules captured at sea and hatched in the lab. The present study confirms their data showing this early stage to have a 3-D rachidian. Possession of a 3-D-type rachidian during any stage of ontogeny in a rapanine is unusual because previous studies of radular ontogeny of rapanines and a nested subclade within the Rapaninae, the Ergalataxinae, have reported only the flat rachidian type at any stage of development (Fujioka 1984a, 1984b, 1985a). However, given the size range of juvenile rapanines examined by Fujioka, it is possible that this stage of ontogeny was overlooked.

The transition from 3-D to dagger-type rachidian occurs after metamorphosis (DiSalvo, pers. comm.) and between shell lengths of 4 and 11 mm (this study).

Subfamily TROPHONINAE

Trophon geversianus (Pallas, 1774)

(Figs. 6A-D)

Material examined

Research material for *Trophon geversianus* (Pallas, 1774) was obtained from dried and alcohol-preserved specimens in the personal collection of E. H. Vokes (Tulane University). This material included ten dried pre-hatched juveniles, all less than 2 mm in shell length, removed from a single egg capsule collected at a beach at Río Grande, Tierra del Fuego, Argentina. Although not yet hatched, the animals appear to have undergone metamorphosis, as indicated by the initiation of teleoconch (adult) sculpture. Also sampled were twenty alcohol-preserved adult specimens (all > 30mm) from Bahía El Pescador, south of Puerto Pirámides, in the northeastern part of Golfo Nuevo, Argentina. This collection was also from the collection of E. H. Vokes.

Ontogeny

In post-metamorphic, pre-hatched juveniles of this species, the rachidian tooth is approx. 10 μ m in width and has a 3-D morphology (Figs. 6A-B). The intermediate denticle is long and has an attachment site on the rachidian base independent of the lateral cusp but closer to the lateral than the central cusp. The basal region is rectangular and deep, with a strong marginal cusp and a second bud-like cusp closer to the radular ribbon.

Rachidian teeth in adults sampled are approx. 200 μ m in width and exhibit a dagger-type morphology (Figs. 6C-D). The intermediate denticle is shorter than in early ontogeny (only one-fifth the height of the lateral cusp) and fused with the lateral cusp instead of having a separate attachment site on the rachidian base. The outer edges of the lateral cusps possess small serrations or outer lateral denticles. The basal end-point is rectangular but shallow and marked by a single marginal cusp. The second bud-like cusp of early ontogeny is obsolete or nearly so.

Remarks

Several authors have published line drawings and scanning electron micrographs of the radulae of adult *Trophon geversianus*, including Radwin and D'Attilio (1976), Kool (1993a), and Pastorino (2002). The present study is the first to document the morphology of the rachidia in early post-metamorphic individuals.

Subfamily OCENEBRINAE

Urosalpinx cinerea (Say, 1822)

(Figs. 7A-D)

Material examined

Specimens of the ocenebrine muricid *Urosalpinx cinerea* were obtained in May 2001 from intertidal barnacle, mussel, and bryozoan-encrusted rocks from a jetty in San Francisco Bay in Burlingame, California, USA. This species is native to the western Atlantic, but was introduced to the eastern Pacific nearly a century ago (Radwin and D'Attilio 1976). Twenty large adults (20-30 mm), including both males and females, were collected at the Burlingame locality and preserved immediately in 75% ethanol for later dissection. Another 10 individuals were placed in a single aquarium with recirculating seawater and provided with barnacles for food. Within days, adult snails deposited egg capsules on tank walls. After approx. six weeks, several hundred hatchlings (1.5-2.0 mm shell length) emerged from the capsules as crawl-away juveniles and began drilling barnacles provided and cannibalizing one another by drilling. Approximately 50 hatchlings were harvested immediately and preserved in 75% ethanol.

Ontogeny

Animals ~2.0 mm in shell length possess rachidia 10 μ m in width with a 3-D morphology (Figs. 7A-B). Adult rachidia are larger (approx. 100 μ m) but nearly identical in shape (Figs. 7C-D).

Remarks

Radwin and D'Attilio (1976) and Kool (1993b) illustrated the adult radula of *Urosalpinx cinerea*, but there have

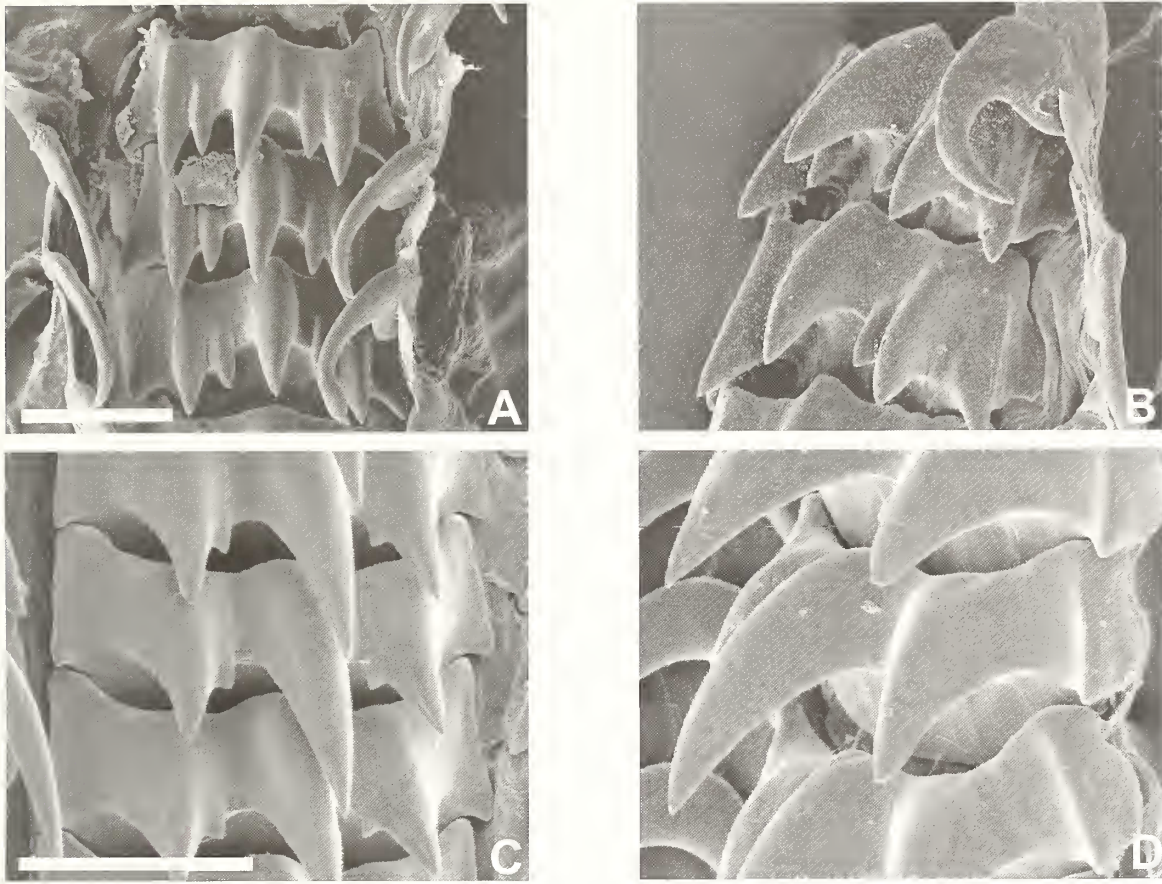


Figure 6. Radular ontogeny of the trophonine muricid *Trophon geversianus*. A-B. Front and lateral views of rachidia of early post-metamorphic (pre-hatched) individuals with shell lengths of 1.5 to 2.0 mm, locality: Tierra del Fuego, Argentina, scale bars = 10 µm. C-D. Front and lateral views of rachidia of adult specimen with shell length of 30 mm, locality: Golfo Nuevo, Argentina, scale bar = 100 µm.

been no studies of radular morphology during early ontogeny. Carriker (1969) figured the mature radula of a subspecies, *Urosalpinx cinerea* var. *etterae* Baker, 1955, including eight scanning electron micrographs of radulae from various angles and two light micrographs of a rasping radula in the process of drilling a shell. The radula of this subspecies appears to differ from that of the nominate form in having one or two extra marginal denticles.

Subfamily MURICOPSINAE?

Vitularia salebrosa (King and Broderip, 1832)
(Figs. 8A-I)

Material examined

One dried juvenile specimen of *Vitularia salebrosa* (9.9 mm shell length) and ten dried adult specimens (30-50 mm shell length) from various tropical eastern Pacific localities were obtained from the personal research collections of E. H.

Vokes and G. J. Vermeij. No other specimens of this species were available at the time the study was conducted.

Ontogeny

At the small juvenile stage (one 9.9 mm specimen), the rachidian is just over 5 µm in width and resembles the 3-D type in having a short, beak-like central cusp (Figs. 8A-C). However, the rachidian base is flat rather than rectangular, a condition typically associated with flattened rachidia. Adjacent to the central cusp are three pairs of short, conical "cusps." The intermediate denticle is unusual for the 3-D type in projecting further from the rachidian base than the adjacent "lateral" cusp. The attachment site for the denticle is separate from the lateral cusp as in some muricopsines. The outermost cusp sits far from the margin endpoint, which curves into a pseudo-cusp. The rachidian of a larger specimen (31 mm shell length) differs in having a slightly longer outermost cusp.

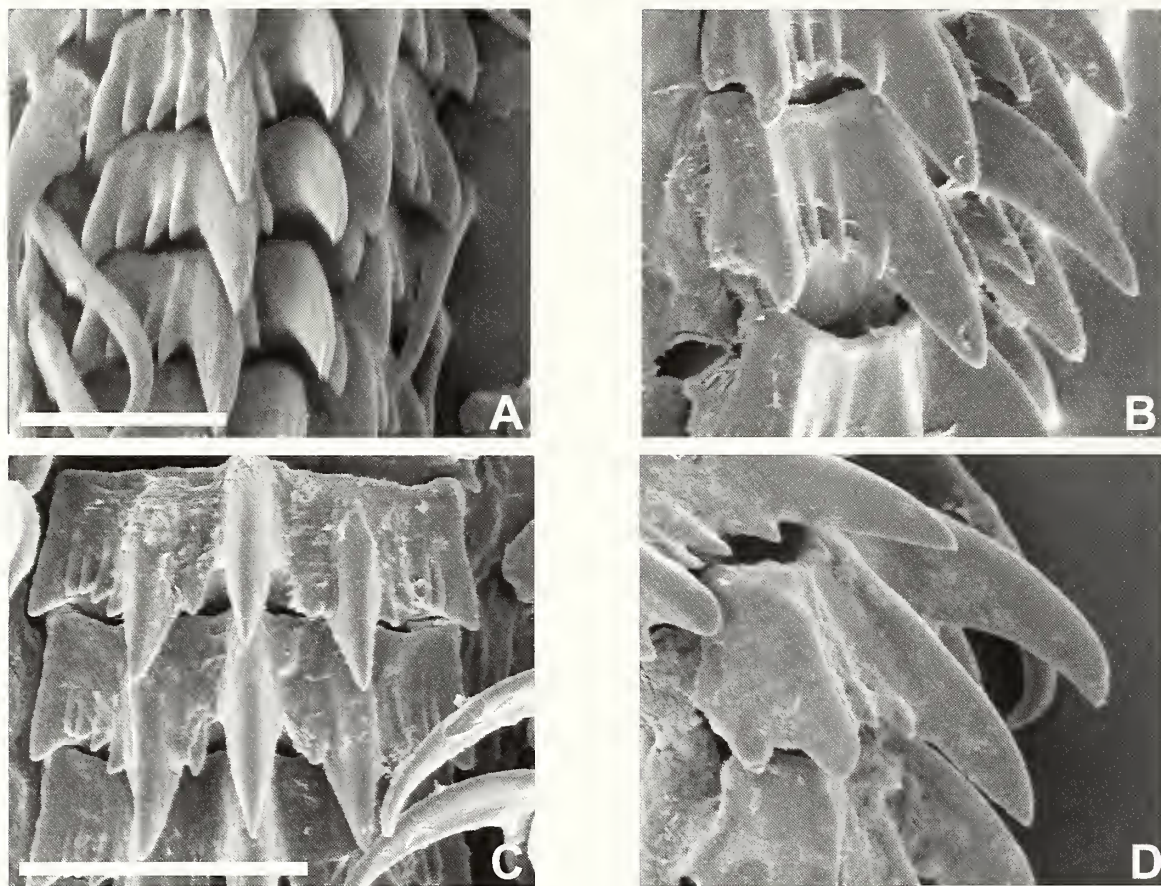


Figure 7. Radular ontogeny of the ocenebrine muricid *Urosalpinx cinerea*. A-B. Front and lateral views of rachidia of early post-metamorphic individuals with shell lengths of 1.5 to 2.0 mm, locality: San Francisco Bay, California, scale bar = 5 μ m. C-D. Front and lateral views of rachidia of adult specimen with shell length of 25 mm, locality: San Francisco Bay, California, scale bar = 50 μ m.

The largest individuals of *Vitularia salebrosa* available to us (40 to 50 mm specimens) failed to produce a radula in eight of the nine specimens we examined (89%). A single radula from a shell 50 mm in length shows rachidian teeth to be approx. 70 μ m in width with long, tusk-like outermost (marginal?) cusps situated far from the base endpoint (Figs. 8G-I). The overall morphology of the central cusp is roughly of the 3-D rachidian type, but the outermost cusps are massive and elongated as in the typical dagger-type rachidian.

Remarks

D'Attilio's (1991) investigation of the radula of *Vitularia salebrosa* showed that this species has at least two different radular morphotypes, including a "normal" rachidian with seven cusps and a second rachidian with only three cusps, which he described as "extremely aberrant resembling nothing else known to me." The latter morphotype has one sub-obsolete central cusp and two massive, incurved, tusk-like lateral cusps. D'Attilio did not provide information on the

sizes of the "normal" and "aberrant" rachidia, but the present data suggest they could represent end-members of a single ontogenetic sequence.

A second "aberrant" feature of the radula of *Vitularia salebrosa* is its occasional absence. D'Attilio (1991) reported that his own efforts to recover a radula from this species were successful only twice out of ten total attempts, which is similar to the success rate of one out of nine attempts reported in this study. This species is parasitic on oysters and attacks by pushing the proboscis between the valve margins, aided initially by drilling (G. S. Herbert and G. P. Dietl, pers. obs.). Attacking oysters at the edge could result in amputation of the proboscis and radular loss when the oyster closes its valves. Another possibility is that the radula is used only to initiate an edge-drilled hole, and afterwards, the animal reabsorbs used teeth and stops forming new ones as it begins a parasitic existence. A major group of muricid parasites, the coralliophilines, lacks a radula, but these are obligate parasites, whereas *V. salebrosa* is not.

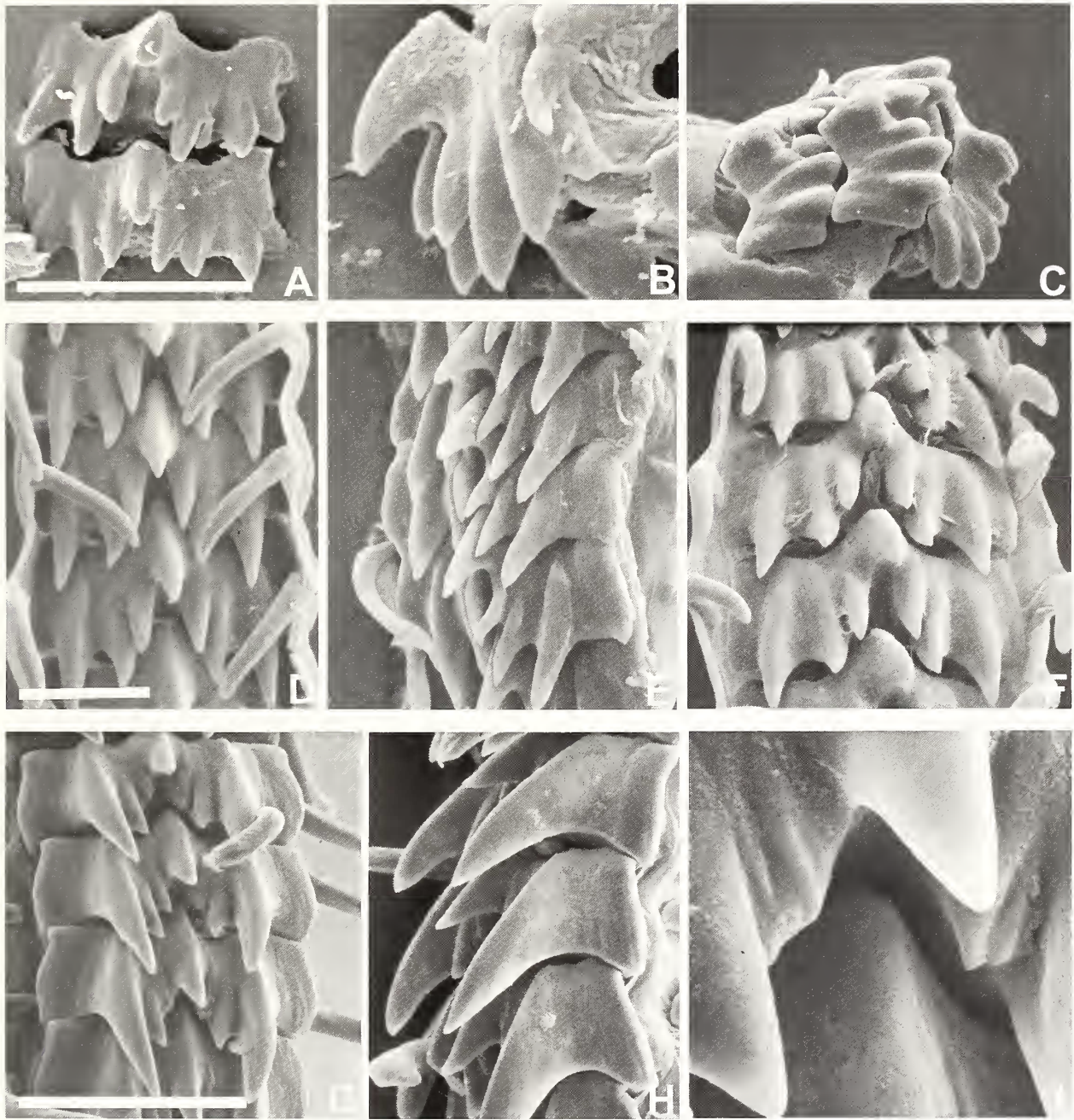


Figure 8. Radular ontogeny of the muricopsine? muricid *Vitularia salebrosa*. A-C. Front and lateral views of rachida of small juvenile with shell length of 9.9 mm, Fig. C shows worn portion of radula presumably used in feeding, locality: Venado Beach, Panama, scale bar = 5 μ m. D-F. Front and lateral views of rachidia of medium-sized juvenile 31 mm in shell length, locality: Venado Beach, Panama, scale bar = 20 μ m. G-I. Front and lateral views of rachidia of mature specimen with shell length of 50 mm, locality: Panama, scale bar = 50 μ m.

We place this species tentatively in the Muricopsinae after Radwin and D'Attilio (1976), although this assignment was and remains controversial due to shell and opercular similarities of this genus to some members of the Ocenebrinae (Vokes 1986). In a cladistic analysis of the Muricidae based on morphological characters of the shell, ovocapsules,

and radula (D. Merle and G. S. Herbert, unpubl. obs.), *Vitularia* is unequivocally placed outside the Muricopsinae and may prove to be a sister group of the Ocenebrinae. Further phylogenetic investigations are necessary to clarify the systematic position of this problematic genus within the Muricidae.

Subfamily MURICINAE

Chicoreus (Phyllonotus) pomum (Gmelin, 1791)

(Figs. 9A-D)

Material examined

Ten adult specimens of the muricine muricid *Chicoreus (Phyllonotus) pomum* were collected from shallow subtidal seagrass beds in December 2002 in St. Joseph's Bay, Florida, USA and transferred to aquaria, where they were monitored and fed regularly. Females deposited communal masses of egg capsules, and offspring hatched within several weeks. Several hundred individuals (1.0-1.5 mm shell length) hatched with a brief pediveliger stage of approx. 24 hours before absorbing the velum and using only the foot for locomotion. After a week, many juveniles began cannibalizing one another by drilling. These fully metamorphosed juveniles were collected then and preserved in 75% ethanol. Five adults (60-70 mm shell length), including males and females,

were also preserved in ethanol after being relaxed in a 7.5% isotonic solution of magnesium chloride.

Ontogeny

Early post-metamorphic juveniles (1.0-1.5 mm shell length) have a rachidian that is 15 μm wide and has only three cusps of similar lengths and lying in the same plane, with intermediate denticles usually absent (Figs. 9A-B). Each rachidian of an adult snail is roughly 200 μm in width, and has a wider base, more massive cusps, a new intermediate denticle, and a more elongate central cusp (Figs. 9C-D).

Remarks

Radwin and Wells (1968) and Radwin and D'Attilio (1976) figured line drawings of the mature radula of *Chicoreus (Phyllonotus) pomum*. There are no other published illustrations of the early post-metamorphic or juvenile stage radular morphologies of this species.

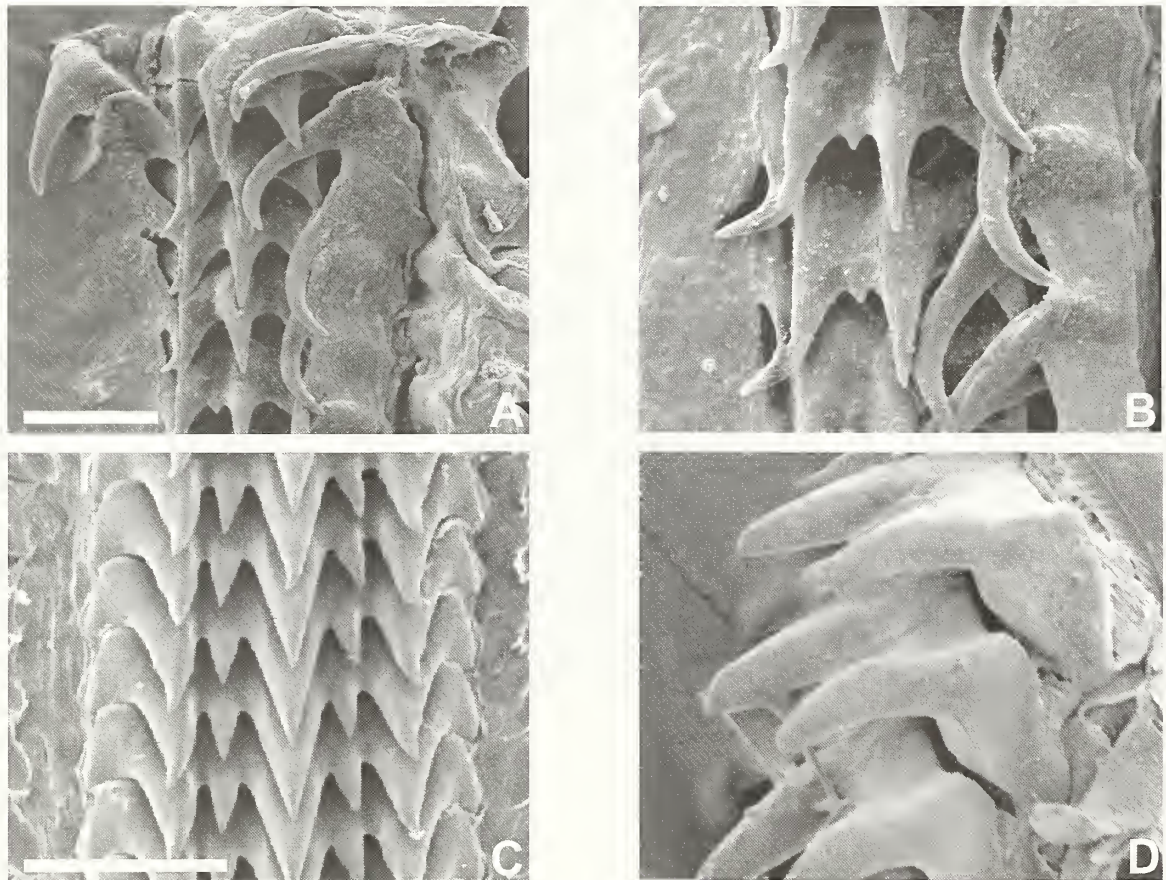


Figure 9. Radular ontogeny of the muricine *Chicoreus (Phyllonotus) pomum*. A-B. Front views of rachidia showing irregular presence of intermediate denticle in an early post-metamorphic individual with shell length of 1.5 mm, locality: St. Joseph's Bay, Florida, scale bar = 10 μm . C-D. Front and lateral views of rachidia of mature individual with shell length 63 mm, locality: St. Joseph's Bay, Florida, scale bar = 100 μm .

The absence of intermediate denticles and overall appearance of the rachidian in young individuals of *Phyllonotus pomum* gives this radular element a generalized neogastropod or "buccinoid" appearance. Similar rachidia occur in buccinids but also in olivids, melongenids, and turbinellid neogastropods, for example. Most interesting is the fact that this rachidian type has not been documented previously within the Muricidae. It is the first-known link in rachidian form between muricids and non-muricids.

DISCUSSION

Fujioka (1982, 1984a, 1984b, 1985a, 1985b) was the first to report that the muricid radula has the capacity to undergo

radical transformation between subfamily-level bauplane during ontogeny. He found, specifically, that the ergalataxine monocusped rachidian likely evolved through peramorphic heterochrony, *i.e.*, extension of an ancestral rapanid ontogeny characterized by progressive reduction of all but the central cusp. With the exception of a brief treatment of the radular ontogeny of the muricine *Chicoreus* (*Triplex*) *torrefactus* by Houart (1992), however, we have, until now, known nothing of the ontogenies of the radulae of other muricids.

The present study demonstrates that major transformations between radular bauplane are nearly pervasive within the Muricidae, with transformations occurring in four of the five subfamilies studied (Fig. 10). The ontogeny of *Phyllonotus pomum* also links the seemingly disparate rachidian

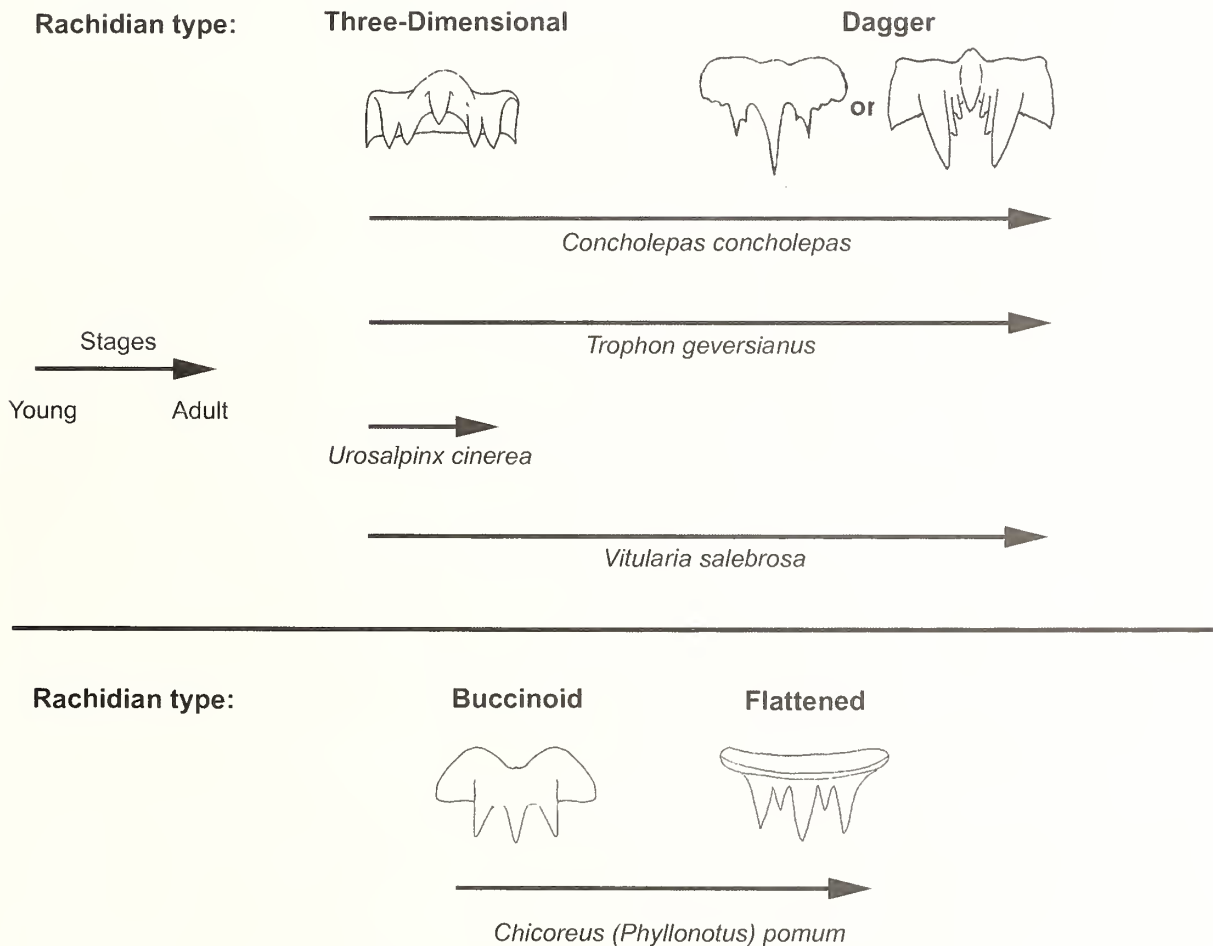


Figure 10. Generalized patterns of radular ontogeny in five species of muricid gastropod. A-B. Most of the species studied herein begin ontogeny with the three-dimensional rachidian tooth as found in the Ocenebrinae and Muricopsinae but end with a dagger rachidian typical of the Rapaninae and Ergalataxinae as well as some Trophoninae and the *Thais*-like Ocenebrinae (*i.e.*, *Nucella*, *Acanthina*, etc.). C-D. One species, *Phyllonotus pomum*, begins ontogeny with a generalized neogastropod ("buccinoid") rachidian and shifts to a flattened, pentacused rachidian with intermediate denticles typical of the Muricidae.

morphologies of muricid and non-muricid neogastropods, and suggests that the primitive, pentacusped rachidian of the Muricidae evolved through extension of development. Equally interesting is the widespread occurrence of the 3-D rachidian that, until now, has been considered a defining trait of only the Muricopsinae and the Ocenebrinae. Data presented or reviewed in this paper demonstrate that the 3-D rachidian also occurs in at least some species of the Muricinae [*Chicopinnatus* and *Chicoreus (Triplex)*], Rapaninae (*Concholepas*), and Trophoninae (*Trophon*).

Feeding observations for one of the species studied, the rapanine *Concholepas concholepas*, suggest that the 3-D rachidian could be a functional specialization for scraping against hard substrata, whereas the dagger-type rachidian that occurs later in ontogeny could be specialized for non-drilling modes of prey subjugation. Individuals of *C. concholepas* drill shelled prey or rasp rock surfaces in search of algae exclusively during their early post-metamorphosis stage, when the animal has the 3-D rachidian, but shift to attacking prey by stabbing or lacerating the soft parts with the radula through natural orifices by the time they reach 10 to 15 mm in shell length, when it has the dagger-type rachidian (Castilla *et al.* 1979, Paine and Suchanek 1983, DiSalvo 1982, 1988, Dye 1991, DiSalvo and Carriker 1994).

Muricids that possess a 3-D rachidian as adults, *i.e.*, most species of the Ocenebrinae and Muricopsinae, also use drilling as their primary or exclusive mode of attack (G. S. Herbert, pers. obs.), again tying this rachidian bauplan to a specific drilling function. Ocenebrine and muricopsine muricids also tend to be exceedingly small relative to other taxa in the Muricidae and, thus, most similar ecologically to juvenile rather than large adult individuals of *Concholepas concholepas*. It may well be that young or small muricids lack the power to incapacitate prey using faster techniques, such as toxins or the brute force of chipping and prying (Herbert 2004), thus requiring slower methods for feeding such as drilling (Dietl and Herbert 2005) and, hence, a specialized radular type. Studies using computer modeling of the various radular morphologies within the Muricidae will be necessary to understand the exact functional basis of these radular types.

It is striking that essentially the same ontogenetic trend toward a more flattened rachidian base and elongation of just one or two cusps occurs in species that differ at all stages in important details of cusp number, position, and shape. Such differences suggest that basic structural similarities (*i.e.*, 3-D vs. flattened vs. dagger forms) among adult rachidia may be the result of independent innovation. Once the first 3-D-to-dagger ontogenetic trajectory evolved, any descendent lineages possessing this generalized ontogeny would have had the opportunity to retain the 3-D rachidian

into adulthood independently through evolutionary truncation or a slowing of development. For these reasons, it is important to revisit past systematic assignments based on the bauplane that are the focus of the present study (see background section).

The repeated evolution of new traits, or innovations, has been a central theme of the muricid radiation (Vermeij 1998, 2001, Marko and Vermeij 1999, Vermeij and Carlson 2000), perhaps more so than in any other neogastropod clade. Although this phenomenon has been examined in the past from the standpoint of extrinsic factors, such as environmental conditions (*e.g.*, temperature, productivity) and community dynamics (*e.g.*, presence of incumbents, competition intensity), the ontogenetic data presented herein point to a complementary process, namely the evolution of developmental timing. Major morphological transformations during ontogeny increase the amount of phenotypic variation in the population upon which natural selection can act and, thus, the intrinsic capacity of a species to create new characters or transform existing ones. They can also reduce genetic constraints on repetitive innovation by allowing morphologies or structures already present at one stage of development to shift to later (or earlier) stages through small-scale changes in the rate or timing of development.

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